

**A DENSITY-DEPENDANT MODEL OF POPULATION DYNAMICS
TO INVESTIGATE THE IMPACT OF THE EUROPEAN ALBACORE TUNA
DRIFTNET FISHERY ON DOLPHINS POPULATIONS**

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Abstract

Common and striped dolphins are part of the bycatch of the European albacore tuna driftnet fishery off the bay of Biscay. In order to investigate the impact of these dolphins incidental catch at the population level, a population dynamics model is developed based on a Leslie matrix which coefficients are given by density-dependent models of reproduction and survival rates.

Capacity for these population to sustain the additional mortality due to the driftnets is assessed with different hypotheses on the choice and the number of density-dependent parameters. Equilibrium level (when they occur) are also calculated depending on the intensity of the density-dependence and compared with the maximum net productivity level.

Results of these simulations show that population growth rate figure can be defined as a management criteria with biological significance, and that such a model could be used to test management scenarios for marine mammals species.

Résumé

Les dauphins communs et les dauphins bleu et blanc font partie des captures accessoires de la pêcherie européenne de thon germon au filet maillant dérivant au large au golfe de Gascogne. Afin d'étudier l'impact de ces captures accidentelles sur ces populations de dauphins, un modèle de dynamique des populations est développé, basé sur une matrice de Leslie dont les coefficients sont obtenus à l'aide de modèles densité-dépendants des taux de reproduction et de survie.

La capacité de ces populations à supporter la mortalité additionnelle engendrée par les filets maillants dérivants est estimée avec différentes hypothèses combinaisons de paramètres densité-dépendants. Le niveau d'équilibre (lorsqu'il est atteint) est également calculé en fonction de l'intensité de la densité-dépendance, et comparé au niveau de productivité maximale.

Les résultats de ces simulations montrent que la valeur du taux d'accroissement de la population peut définir des critères de gestion ayant une signification biologique, et qu'un tel modèle pourrait être utilisé pour tester différentes mesures de gestion des stocks de mammifères marins.

Introduction

Over the world, several fisheries are confronted with the problem of cetacean bycatch, and the impact that these fisheries could have on the cetacean population has been the object of many recent publications (Woodley, 1993 ; Barlow, 1989). And in 1992, the problem of dolphin bycatch led the European Communities Council to reglement the use of driftnets in community waters, and especially for the albacore tuna driftnet fishery off the bay of Biscay. A sampling program was conducted on board the driftnetters and additional mortality due to the French albacore tuna driftnet fishery was estimated for common and striped dolphin (Goujon, 1996).

Two questions arises in this paper: the first one concerns the impact of this additional mortality on dolphins population, and the second one is to know whether density-dependent phenomenon, if they exist, can compensate this mortality and make it sustainable for the dolphins population. To address these questions, a population dynamics model is built and different possibilities of density-dependence are investigated.

The model of dolphin population dynamics

The model is based on a Leslie matrix (Leslie, 1945) which coefficients depend on density-dependant parameters. Therefore it is a combination of 4 components that are modelizing the density-dependence, the survival rates, the reproduction rates and the dynamics of dolphins (figure 1).

The Leslie matrix

The Leslie matrix are often used to modelize marine mammals population dynamics in order to produce population growth rates estimates for management objectives (Eberhardt, 1985 ; Reilly and Barlow, 1986). The Leslie matrix (L) can be expressed as:

$$L = \begin{bmatrix} tr(1) & tr(n-1) & tr(n) \\ ts(1) & 0 & 0 \\ \vdots & \vdots & \vdots \\ 0 & ts(n-1) & 0 \end{bmatrix} \quad (\text{eq. 1})$$

where $tr(i)$ is the annual reproductive rate at age i , and $ts(i)$ is the annual survival rate at age i .

The population vector at time $t+1$ can then be obtained by scalar multiplication of the population vector at time t :

$$\vec{N}_F(t+1) = L \cdot \vec{N}_F(t) \quad (\text{eq. 2})$$

where $\vec{N}_F(t)$ represents the population vector at time t .

Since sex-ratio is assumed to be equal to 1:1, the model only considers females and the age-specific reproductive rates are divided by 2 in the global model.

Survival rates model

In this paragraph, only natural mortality is taken into account. Survival rate of age class i , $ts(i)$, are defined as the proportion of animals from the previous age class ($i-1$) surviving their i^{th} year. To modelize these survival rates, we use the model of Siler (1979), which assumes that the total risk of mortality at a given age is the sum of an exponentially decreasing risk due to juvenile mortality factors, an exponentially increasing risk due to senescent mortality factors, and a constant risk due to other factors which is predominant during the adult phase (Barlow and Boveng, 1991). Thus, the probability, $l(i)$, of survivorship from birth to age i is expressed as :

$$l(i) = l_j(i) \cdot l_a(i) \cdot l_s(i) \quad (\text{eq. 3})$$

with

$$\begin{cases} l_j(i) = \exp\left(-\frac{\alpha_j}{\beta_j} \cdot \left(1 - \exp\left(-\beta_j \cdot \frac{i}{\Omega}\right)\right)\right) \\ l_a(i) = \exp\left(-\alpha_a \cdot \frac{i}{\Omega}\right) \\ l_s(i) = \exp\left(\frac{\alpha_s}{\beta_s} \cdot \left(1 - \exp\left(\beta_s \cdot \frac{i}{\Omega}\right)\right)\right) \end{cases} \quad (\text{eq. 4})$$

where α_j , β_j , α_a , α_s and β_s are the Siler parameters of the juvenile, the constant (adult) and the senescent mortality.

And, the annual survival rate for each age class is obtained by:

$$ts(i) = \frac{l(i)}{l(i-1)} \quad (\text{eq. 5})$$

In these equations age is divided by the longevity Ω of the animal to make the model general and appropriate over different species (Barlow and Boveng, 1991).

Reproductive rate model

Reproductive rate of age class i , $tr(i)$, is hereafter defined as the number of offsprings born year $t+1$ from females of age $i+1$ divided by the number of females of age i at year t .

A model similar to the Siler model has been developed. It assumes that reproductive rates are the combination of three components :

- the acquisition of sexual maturity during the juvenile phase, which is modeled by a logistic function with the inflexion point corresponding to the average age at first calving (AFC).
- the loss of reproductive potential during the senescent phase, which is modeled by a negative logistic function with the inflexion point corresponding to the average age at reproductive senescence (ARS).
- the reproductive capacity for adult animals, which is supposed to decrease linearly with age from a "maximal" average reproductive rate reached at the end of maturation, arbitrarily set at 1.5 times the average age at first calving, and equal to the maximal fecundity rate (FR_m) divided by the average calving interval (CI) reduced by the proportion of females simultaneously lactating and pregnant (pLP).

Thus, the annual reproductive rate for each age class i is obtained by:

$$tr(i) = tr_j(i) \cdot tr_a(i) \cdot tr_s(i) \quad (\text{eq. 6})$$

where

$$\begin{cases} tr_j(i) = \frac{1}{1 + \exp\left(\varphi_j \cdot \frac{i - AFC}{\Omega}\right)} \\ tr_a(i) = \frac{FR_m}{CI - pLP} \times \max\left(1, 1 - \varphi_a \cdot \frac{i - 1.5 \times AFC}{\Omega}\right) \\ tr_s(i) = \frac{1}{1 + \exp\left(\varphi_s \cdot \frac{i - ARS}{\Omega}\right)} \end{cases} \quad (\text{eq. 7})$$

where φ_j , φ_a and φ_s are the slope parameters of the reproductive model for each of the juvenile, adult and senescent phase.

As in the survival rate model, age is divided by the longevity Ω of the animal to make the model general and appropriate over different species.

Adjustement of the model to obtain a stable population

During 1992 and 1993, observers were embarked on board the tuna driftnetters to identify and count the bycatch and to realize biological sample of the dolphins caught (Goujon *et al.*, 1993). Thus, most of the parameters of the survival model and of the reproduction model were estimated from the data collected during this sampling program, otherwise data from related species were used (Goujon, 1996). Less viable parameters were then tuned within their 50%-estimation confidence interval in order to compensate a slightly negative population growth rate and obtain a stable population as the reference population. Therefore, Goujon (1996) estimates the values of table 1 for the initial parameters of the model.

Table 1. Estimates for the parameters of the survival and the reproduction models used to simulate dolphins population dynamics.

| Parameter (definition, unit) | Common dolphin | Striped dolphin |
|--|----------------|-----------------|
| <i>Reproduction parameters</i> | | |
| FR_m (maximum fecundity rate, in young/female) | 0,93 | 0,92 |
| CI (calving interval, in years) | 3 | 3 |
| pLP (proportion of females lactating & pregnant) | 10% | 10% |
| AFC (age at first calving, in years) | 10,1 | 10,3 |
| φ_j | 30,5 | 30,5 |
| φ_a | 1,26 | 1,36 |
| φ_s | 36,7 | 36,7 |
| ARS (age at reproductive senescence, in years) | 27,1 | 28,5 |
| <i>Survival parameters</i> | | |
| α_j | 16,55 | 13,95 |
| β_j | 55,33 | 31,51 |
| α_a | 0,75 | 0,63 |
| α_s | 0,005 | 0,012 |
| β_s | 8,12 | 7,66 |
| <i>Others parameters</i> | | |
| Ω (longevity, in years) | 30 | 35 |
| $SR0$ (sex ratio) | 1:1 | 1:1 |

Density-dependence model

Leslie matrix based model lead to exponential growth of population, which certainly can not apply to marine mammal populations. In the case of marine mammals, regulatory phenomenon are supposed to modify biological parameters (Eberhardt and Siniff, 1977 ; Fowler, 1987). For instance, a diminution of the average age at sexual maturity and an increase in number of females simultaneously lactating and pregnant have been corelated to the diminution of the striped dolphin population size in the western Pacific (Kasuya, 1985). Similarly, a diminution of average age at sexual maturity was shown for reduced whales population (Lockyer, 1984).

Therefore, density-dependent regulation is introduced to the model according to a generalized logistic model (Verhulst, 1884). Thus, the value $p(t)$ of any density-dependent parameter at time t , is given by:

$$p(t) = p_K + (p_0 - p_K) \cdot \left(1 - \left(\frac{N(t)}{K}\right)^{z_p}\right) \quad (\text{eq. 8})$$

where $N(t)$ is the population size at time t ,

p_K is the value of the parameter at carrying capacity (when $N(t)=K$),

p_0 is the the value of the parameter when the population tends to 0,

z_p is the density-dependent factor.

z_p is assumed to take a value between 1 and 12 (Fowler, 1984). $z_p = 1$ implies a linear

density-dependent whereas $z_p > 1$ implies that the variation of the density-dependent parameter is more important as the population is near carrying capacity.

As for the value of the parameter when the population tends to 0, p_0 , it is assumed to be equal to the biological limit of the parameter, p_{lim} , such as it can be estimated.

Biological parameters are not all density-dependent. Fowler (1987) indicates a density-dependence of reproductive parameters for several cetacean species. Particularly, the maximal fecundity rate and the average age at first calving are considered as being density-dependent for striped and spotted dolphins (Kasuya and Miyazaki, 1982; Kasuya, 1985; Perrin *et al.*, 1977). Moreover, one can expect that additional mortality is to some extent compensated by a diminution of natural mortality due to reduced competition for food resources.

As a consequence, the following parameters will be supposed to be density-dependent: the average age at first calving AFC , the proportion of females simultaneously lactating and pregnant pLP , the Siler parameters α_j and β_j (for juvenile survival) and α_a (for constant or adult survival) and the slope parameter φ_a of the adult reproductive rate.

Biological limits of these parameters and their biological significance are given in table 2.

Table 2. Biological limits of the density-dependent parameters used in the dolphins population dynamics model.

| Parameter | Common dolphin | Striped dolphin | Biological significance |
|-------------|----------------|-----------------|--|
| AFC | 8 | 8 | average age at sexual maturity + 1 year of gestation. |
| pLP | 50% | 50% | corresponding to 100% of lactating females with a 1-year old calf, being pregnant. |
| α_j | 16.55 | 13.95 | corresponding to a juvenile survival rate equals to the square of maximum adult survival rate (the survival of calf times the survival of the mother). |
| β_j | 55.33 | 31.51 | |
| α_a | 0.75 | 0.63 | corresponding to a adult survival rate of 97% (Reilly and Barlow, 1986). |
| φ_a | 0 | 0 | corresponding to a constant adult reproductive rate. |

Method

Additional mortality due to the French albacore tuna driftnet fishery is estimated for all ages combined and also by three age groups: age group 0-2 of 0 to 2-years old juveniles, age group 3-7 of 3 to 7-years old immature animals and age group 8+ of sexually mature adults (Goujon, 1996). Both sets of values of additional mortalities for common and striped dolphins are used to estimates the impact of driftnets (table 3).

Table 3. Estimates of additional mortality of common and striped dolphins used to assess the impact of driftnet on these dolphins populations.

| Age group | Common dolphin | Stiped dolphin |
|-------------------|----------------|----------------|
| all ages combined | 0,78% | 1,81% |
| 0-2 | 2,09% | 5,52% |
| 3-7 | 0,98% | 1,12% |
| 8+ | 0,31% | 0,89% |

Population structure of the initial stable population is first obtained with the model and stored as input for further runs. Two principal outputs of the model are used to characterize the population dynamics: the population growth rate which indicates whether the population has stabilized and the population level at the new equilibrium N_e/K (equals to the population size at

equilibrium, N_e , divided by the carrying capacity, K), which is compared to the maximum net productivity level $MNPL$ (IWC, 1989). In general, runs of 200 years are made, and equilibrium is supposed to be reached when the absolute value of the population growth rate is less than 1‰.

In terms of population management, it is important to consider the population level of the new equilibrium of the new equilibrium (if any) compared to the carrying capacity K or to the $MNPL$. For instance, the american marine mammal protection act fixed a maximum dolphin mortality level for the eastern tropical Pacific tuna purse-seine fishery at half the population growth rate at $MNPL$.

Populations are considered as extinct if N_e/K is less than 0.2 although the model is not any more appropriate at these low population levels since other compensatory phenomenon might occur (Fowler and Baker, 1991).

Three particular values of z_p are used: $z_p=1$ for a linear density-dependence, $z_p=2,4$ as in Chivers and DeMaster (1993) and $z_p=5$, for which the density-dependent parameter varies significantly when the population size is between 60% and 100% of the carrying capacity. When only one parameter is density-dependent, these values lead to a maximum net productivity level of $0,5 \times K$, $0,6 \times K$ and $0,7 \times K$.

Density-dependent responses of the dolphins populations are qualified by the values of density-dependent parameters at new equilibrium.

Because parameters can not take values beyond their biological limit, we define for each density-dependent parameter a compensatory capacity as the maximum value of additional mortality that can be compensated by density-dependence of the parameter (the other parameters being constant). Similarly, we calculate a cumulative compensatory capacity for two or more simultaneous density-dependent parameters

Results

Impact of the additional mortality due to driftnets without density-dependence

When additional mortality is applied without any compensatory density-dependence, population growth rates of dolphins populations are equal to -0.7% for common dolphin and -1.7% for striped dolphin, whether the additional mortality estimates are stratified by age-group or not. Assuming an increase in fishing effort of 30% in order to consider the European albacore tuna driftnet fishery, population growth rates decrease to -1,1% and -2,3% respectively for common and striped dolphins. However, only the additional mortality due to the French driftnetters will be considered hereafter.

The model also shows that, if no compensation phenomenon occurs, the striped dolphin population should be reduced to half its original size in 30 years with such a level of effort (which is not any more the case since net length have been reduced to 2.5 km, versus an average of 7 km initially and since a license system has been developped to limit the number of vessels). Twice this time is necessary to reduce by half the common dolphin population.

Additional mortality compensation by density-dependence of a single parameter

The compensatory capacity of each parameter compared to the value at carrying capacity are given in table 4:

Table 4. Parameters compensatory capacities.

| Parameter | Common dolphin | Striped dolphin |
|-------------|----------------|-----------------|
| AFC | 1.2% | 1.2% |
| pLP | 0.9% | 0.9% |
| φ_a | 0.9% | 0.9% |
| α_j | 0.9% | 1.8% |
| β_a | 1.6% | 2.1% |
| α_a | 2.3% | 1.3% |

According to this table, one can conclude that, in the case of striped dolphins, compensation by modification of the juvenile survival rate parameters is the only one that can compensate the additional mortality due to the French driftnets (which implicates a population growth rate of -1.7%). In the case of common dolphins, all density-dependent parameters can compensate the additional mortality (which implicates a population growth rate of -0.7%).

However, Ne/K depends on the values of the density-dependent factor z_p and of the limit value of the parameter when the population tends to 0, p_0 , as illustrated in figure 2. If p_0 is fixed at p_{lim} as assumed previously, one can see that the density-dependent response on the average age at first calving to compensate additional mortality of common dolphins (upper part of figure 2) brings the population at a level between 35% and 85% of the carrying capacity depending on the value of z_p . Thus, to obtain an equilibrium such that $Ne/K > MNPL$, one must suppose that $z_p > 2.4$. In the case of striped dolphin (lower part of figure 2), the compensation by density-dependence of the Siler parameter β_j is always such that the equilibrium level is higher than the $MNPL$ unless p_0 is smaller than p_{lim} .

The model was also used to show that the higher is the value of z_p , the higher is Ne/K and also the faster the equilibrium is reached, as shown in table 5. In the same way a larger difference between p_0 and p_K increases the population level at equilibrium, and decreases the time necessary to reach it.

Table 5. Values of density-dependent parameters at new equilibrium, p_{Ne} , population level at new equilibrium Ne/K and number of years necessary to reach this equilibrium, NY , with an additional mortality of 0.5% only for striped dolphin and with $p_0 = p_{lim}$.

| Parameter | p_K | p_{Ne} | z_p values | | | | | |
|-------------|-------|----------|--------------|------|--------|------|--------|------|
| | | | 1 | | 2,4 | | 5 | |
| | | | Ne/K | NY | Ne/K | NY | Ne/K | NY |
| AFC | 10,3 | 9,5 | 62% | 169 | 80% | 67 | 90% | 30 |
| pLP | 10% | 32% | 75% | 91 | 89% | 37 | 94% | 20 |
| φ_a | -1,36 | -0,67 | 57% | 226 | 75% | 93 | 87% | 43 |
| α_j | 13,95 | 11,4 | 74% | 100 | 88% | 40 | 94% | 20 |
| β_j | 31,51 | 38,4 | 95% | 18 | 98% | 11 | 99% | 6 |
| α_a | 0,75 | 0,46 | 66% | 148 | 83% | 61 | 91% | 29 |

Additional mortality compensation by density-dependence of more than one parameter

Cumulative compensatory capacity for two or more simultaneous density-dependent parameters are given in table 6:

Table 6. Cumulative compensatory capacities intervals.

| Number of simultaneous density-dependent parameters | Cumulative compensatory capacity interval |
|---|---|
| 1 | 0,9% - 2,3% |
| 2 | 1,7% - 3,6% |
| 3 | 2,9% - 4,6% |
| 4 | 4,2% - 6,0% |
| 5 | 6,2% - 6,6% |

According to table 6, up to 6.5% of annual population decrease due to additional mortality can be compensated when 5 or 6 parameters (α_j and β are correlated) are simultaneously density-dependent.

Moreover, the population size at equilibrium increases with the number of simultaneous density-dependent parameters. As shown by figure 3, the population size at equilibrium is always greater than the *MNPL* when 4 or more parameters are simultaneously density-dependent. Population level N_e/K of 0,2 is also indicated on this figure to indicate cases where species extinction is probably occurring.

When all the considered parameters are simultaneously density-dependent with the value of the parameter when the population tends to 0, equal to the biological limit of the parameter ($p_0=p_{lim}$) and with the density-dependent factor z_p equal to 1, parameters values at equilibrium are those given in table 7 for striped dolphins.

Table 7. Values of density-dependent parameters at new equilibrium, p_{N_e} when all 6 density-dependent parameters are simultaneously compensating additional mortality for striped dolphins, with all z_p values equal to 1 and $p_0=p_{lim}$.

| Parameter | p_{N_e} | p_K |
|-------------|-----------|-------|
| <i>AFC</i> | 9.7 | 10.3 |
| <i>pLP</i> | 12.9% | 10% |
| φ_a | 1.16 | 1.36 |
| α_j | 12.5 | 13.95 |
| β_a | 50.3 | 31.51 |
| α_a | 0.54 | 0.63 |

For striped dolphins, equilibrium is reached after about 20 years at a level of 83% of the carrying capacity. Average adult reproductive rate and survival do not change significantly and the juvenile (first year) survival rate rises from 0.75 to 0.81. For common dolphins, the population level at new equilibrium (reached in less than 20 years) represents 88% of the carrying capacity.

Discussion

Simulation appears to be a convenient mean to study the impact of bycatch of the albacore tuna driftnet fishery on dolphin population. Although the results obtained might not describe exactly the real evolution of dolphin population, they are probably of the same order of magnitude. The simulation also allows to determine clearly the important dynamic or biological parameters that influence the population growth rate and that should be investigated in the future. Finally, the simulation reveals the relationship between the equilibrium level and the density-dependence factors (the value of the parameter when the population tends to 0, p_0 and the z_p factor).

Dolphin additional mortality

The estimates of annual population decrease due to the driftnets, which is equal to population growth rate when additional mortality is applied without compensatory phenomenon, are similar to that found by Goujon *et al.* (1993) and Woodley (1993), using Leslie matrix which coefficients were not modeled.

In its Special Issue 15 (IWC, 1994), the International Whaling Commission (IWC) seems to have used the values of an additional mortality of 2% and 4% as criteria to qualify the impact of bycatch on dolphins populations as sustainable, potentially unsustainable or unsustainable. According to this, one can say that the impact of the European albacore tuna driftnet fishery is sustainable for common dolphins and potentially unsustainable for striped dolphins. The approach of the IWC is similar to consider that: 1) density-dependence of a single dynamic or biological parameter is commonly accepted (up to a 2%-compensation); 2) that to compensate more than about 2% of annual decrease, one has to assume 2 or more simultaneous density-dependent

parameters which might not be the case; 3) that assuming more than 3 density-dependent parameters (to compensate more than 4% of annual decrease) is considered as unreasonable. However, the model shows that if 4 or more parameters are simultaneously density-dependent, then the IWC limit appears conservative since up to 6.5% of annual population decrease can be compensated. Moreover, the model shows that additional mortality (all age combined) can differ up to 33% from the annual population decrease (in both ways). In fact, if the dolphins caught by the driftnets are all adults, then an additional mortality of 1% would lead to an annual population decrease of 0.8%, whereas, if the dolphins are all juveniles of 3 to 7-years old, the annual population decrease would be of 1.33%.

The results of the simulations also suggest that more in-field measures and computer simulations should be done in order to estimate what are truly the possibilities of compensation of marine mammals in terms of number of density-dependent parameters and of density-dependent factors for these parameters. Such simulations should also be used to investigate whether the evolution of some key biological indices, or combinations of these, can be correlated to the population level, as suggested by Fowler and Siniff (1992). The average age at first calving, the proportion of females simultaneously lactating and pregnant, the juvenile or adult survival rate might be some of those biological indices. Sex-ratio might also be considered as a possible parameter likely to compensate additional mortality, what has not been investigated in this study.

Nevertheless, density-dependence is a complex phenomenon. Beyond the fact it is probably not linear, density-dependence might also be a delayed response to population dynamics changes. When several parameters are supposed to be density-dependent, it becomes then more difficult to identify the evolution of each parameter, which will have different density-dependent factors (Taylor and DeMaster, 1993) and occur with different delays. For instance, a sudden drop in population size (such as it can occur after an epizootic event) will lead to an important increase in food resource and then in a low natural mortality for both juveniles and adults. This passive density-dependent reaction will further imply that, after a few years, there might be an over-abundance of sexually mature animals that will then be compensated by a delayed age at first calving or a stretching of the calving interval. Thus, the population does not evolve to the equilibrium in a straight way but with oscillations, which can explain that inconsistent parameter evolution has been observed as mentioned by Barlow (1985) and Chivers and DeMaster (1994).

Then, bioenergetics should also be considered when trying to determine the occurrence and the magnitude of density-dependent responses to additional mortality or food resource change. Finally, one should not forget that dolphins and tunas have overlapping diets and that tuna abundance could also affect the density-dependence of dolphins populations.

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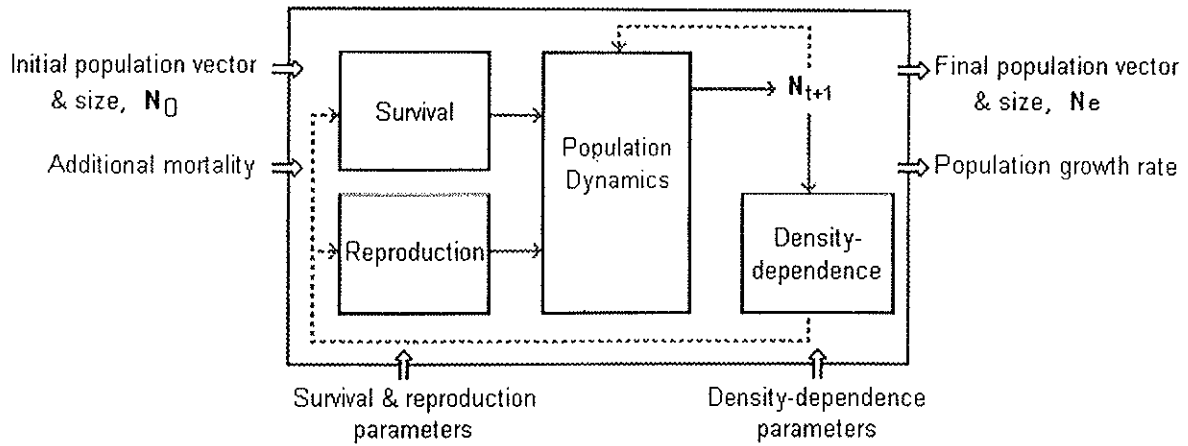


Figure 1. Schematic representation of the population dynamics model developed to assess the impact of driftnets on common and striped dolphins populations off the bay of Biscay.

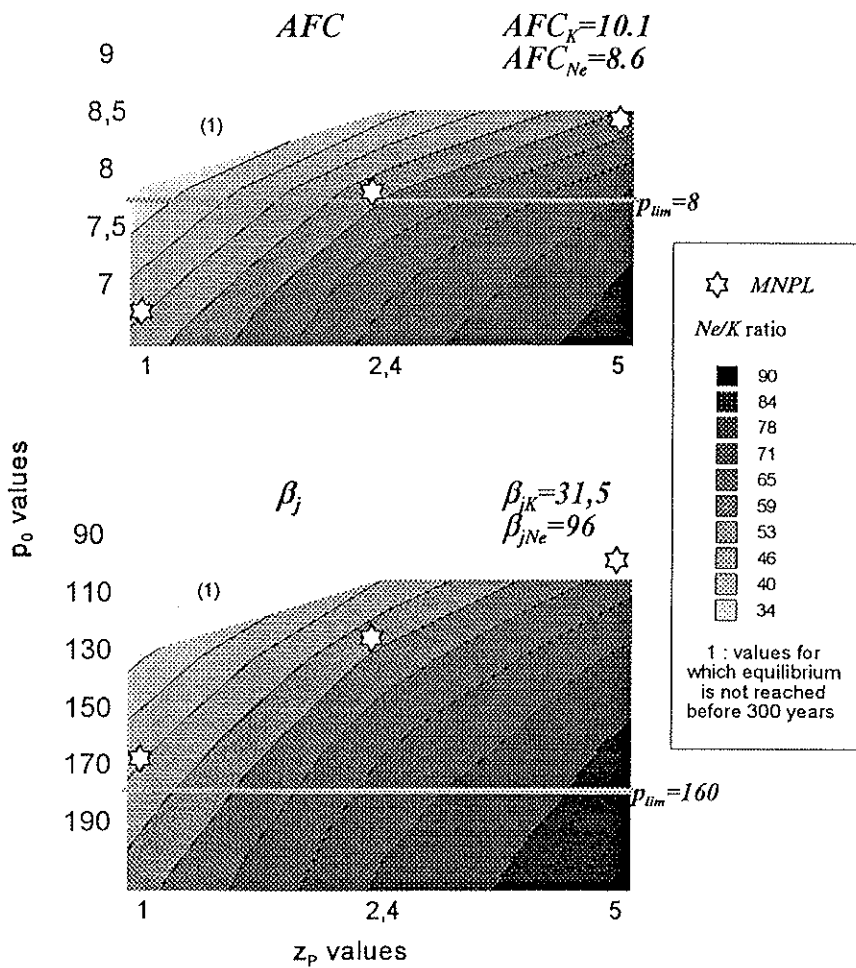


Figure 2. Evolution of Ne/K as a function of the factors z_p and p_0 for two density-dependent parameters: the average age at first calving AFC compensating the common dolphin population growth rate of -0.7% (upper part) and the juvenile survival parameter β_j compensating the striped dolphin population growth rate of -1.7% .

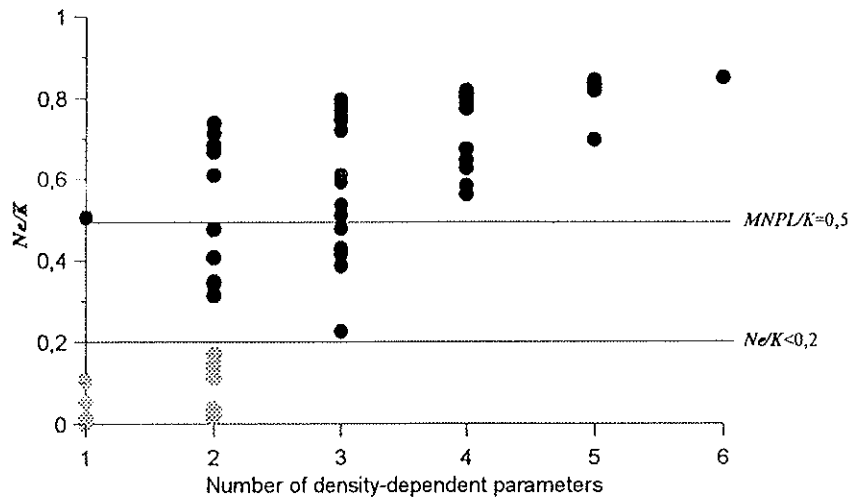


Figure 3. Evolution of Ne/K with the number of density-dependent parameters to compensate the striped dolphin population growth rate of -1,7%. For all parameters, the density-dependence factors are $z_p=1$ and $p_\delta=p_{lim}$.